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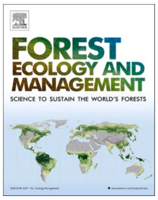

Early and repeated nutrient additions support far greater stemwood production in Norway spruce than traditional late-rotation fertilisation

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ABSTRACT

Silvicultural techniques aimed at promoting forest biomass production can help meet the growing demand for renewable materials and mitigate climate change. One-time nitrogen (N) addition late in the rotation is a well-established method to stimulate growth in coniferous forests in northern Europe, but the potential gains from earlier and repeated fertiliser application remain uncertain. Here, we tested the impact of repeated fertilisation in juvenile Norway spruce stands across 9 sites covering a wide range of growing conditions over a 700 km stretch from central to southern Sweden. We tested the fertilisation effects using two separate studies: i) an interval trial with a fertilisation frequency of one (F1), two (F2), or three years (F3) performed at plot-level across five sites (2002–2014), and ii) a practice-oriented trial with a two-year fertilisation interval (F2) applied at stand-level and replicated at four sites (2003–2013). The composition of the nutrient mix in each plot was optimised based on foliar nutrient analyses. In the interval trial, all three fertilisation schedules strongly increased periodic annual increment (PAI) (F1: 105 %, F2: 93 %, F3: 79 %) relative to the unfertilised control, resulting in more than a doubling of stem volume yield in the F1 and F2 treatments (120 % and 110 %, respectively) and a significantly smaller but still sizeable yield stimulation of 82 % in the F3 treatment. Nitrogen use efficiency (NUE, stemwood volume increase per unit mass of N added) was similar among fertilisation intervals (on average 130 m^3 ha^{-1} 1000 kg N^{-1}), indicating that the extra N provided through yearly fertilisation (F1) is redundant given the similar stemwood yields in the F2 treatment. In the practice-oriented trial, the sole F2 treatment increased PAI by 95 % over the control, translating into a yield stimulation of 114 % and an almost identical NUE to that of the interval trial. NUE greatly exceeded the figures typically observed with traditional late-rotation fertilisation and correlated inversely with baseline site productivity (using site index as a proxy) in the F1 and F2 treatments (the latter pooled across the two trials). Our results clearly indicate that nutrient limitation restricts growth and carbon (C) capture in young Norway spruce plantations in northern Europe to less than half of their potential, highlighting repeated fertilisation at nutrient-poor sites as an effective management tool to support a growing bioeconomy and enhance C sequestration.

1. Introduction

Forests and the wood they produce play a key role in mitigating climate change and in the current transition to a biobased economy (Lundmark et al., 2014; Sathre et al., 2010; Sathre and O'Connor, 2010; Schulze et al., 2020). The growing demand for forest products and services and emerging conflicts over limited land resources, call for developing strategies to increase the supply of resources and forest ecosystem services at the landscape-level. For example, the Swedish forest industry consumed ca. 80 million m^3 of roundwood in 2019, while the harvested volume was only about 70 million m^3 with an expected increase in consumption by another 5 million m^3 until 2035 (Nordström et al., 2021). Advancing the use of forest products and other ecosystem services hinges on increasing the efficiency of biomass production and promoting innovative approaches to optimise wood and resource utilisation from forests (Regeringskansliet, 2018). Underutilised

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silvicultural methods, such as clonal forestry, reforestation with exotic species, and fertilisation, have the potential to roughly double the total annual growth in Sweden (Larsson et al., 2009). However, practical constraints such as additional operational costs may reduce the potential to 20 % (Fries and Normark, 2019). Similarly large potential for improvement probably exists throughout northern Europe and the remaining boreal zone (Brockley, 2010; Brockley, 2007; Brockley, 1992; Hedwall et al., 2014b; Kishchuk et al., 2002; Nilsen, 2001).

Forest fertilisation can substantially enhance growth in boreal coniferous forests as these are often limited by nutrients, especially nitrogen (N) (Hedwall et al., 2014b; Nilsen, 2001; Tamm, 1991). In Swedish forestry, fertiliser is most often applied late in the rotation, typically a single application of 150 kg N ha^{-1}, which commonly increases the growth of stemwood by 10–20 m^3 ha^{-1} (~30 %) within a decade in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Bergh and Hedwall, 2013; Nohrstedt, 2001). Phosphorus (P) and potassium (K) usually have no effect when added alone but stimulate additional growth in combination with N (Bergh and Hedwall, 2013; Brockley, 2010; Nohrstedt, 2001). Most fertilisation studies in northern Europe have focused on middle-aged or older forests (Nilsen, 2001; Nohrstedt, 2001; Óskarsson and Sigurgeirsson, 2001; Saarsalmi and Mälkönen, 2001; Vejre et al., 2001). However, N may also be limiting in younger forests, as nutrient demand is likely to be high during early stand development and may thus constrain leaf area expansion and delay canopy closure (Amponsah et al., 2005; Bergh et al., 2005; Brockley, 2010), as suggested by the long time (often decades) required for the canopies of boreal Norway spruce stands to close completely (Bonan, 1993; Goude et al., 2019). Thus, repeated nutrient additions throughout the entire rotation could eliminate nutrient limitations and enhance productivity but uncertainties about the efficiency due to the paucity of relevant data make conventional fertilisation late in the rotation financially less risky (Hedwall et al., 2014b). In addition, concerns about environmental side-effects of repeated fertiliser applications, such as changes in the soil microbial community or understory vegetation and the potentially heightened risk of nutrient leaching into groundwater and streams has further hampered its implementation in boreal forestry (Gundersen et al., 2006; Hedwall et al., 2014b).

Nutrient optimisation is a concept geared towards mitigating these potential side-effects by matching the supply of nutrients to the demand of the trees, thereby maximising growth while minimising leaching losses (Tamm, 1991). Key to the implementation are foliar element mass-ratios which serve as a proxy for stand nutrient status (Bergh et al., 2005, 1999; Linder, 1995) and correlate with root-shoot biomass allocation and leaching below the root-zone (Ågren and Ingestad, 1987; Ericsson, 1995; Ingestad and Ågren, 1991). In practice, tree growth, foliar nutrient ratios and nutrient leaching are monitored to inform the quantity and composition of the fertiliser applied. This method was initially developed for laboratory-grown seedlings (Ågren and Ingestad, 1987; Ericsson, 1995; Ingestad and Ågren, 1991) and later tested in a rigorous experimental setup in Norway spruce forests at three sites in Sweden (Bergh et al., 2005, 1999; Linder, 1995). These early experiments demonstrated that it was possible to boost current annual growth up to 35, 27 and 22 m^3 ha^{-1} in southern, central, and northern Sweden, respectively, with a maximum effect after 15 years (Bergh and Linder, 2006). Optimal fertilisation has also been applied in British Colombia with mixed findings. Results from lodgepole pine (*Pinus contorta*) trials showed that N-addition alone decreased growth, whereas a nutrient mix based on the nutrient optimisation concept increased stem volume by about 40 % within 15 years after the first fertilisation (Brockley, 2007; Kishchuk et al., 2002). For white spruce (*Picea glauca*), Brockley (2010) reported increased growth with addition of N, boron, and sulphur, but a much higher growth response resulted with a complete mix of nutrients. Similar effects have been reported from young coniferous stands fertilised with a complete nutrient mix (Albaugh et al., 1998; Amponsah et al., 2005; Bennett et al., 2003; Hanssen and Kvaalen, 2018). Despite the demonstrated growth-stimulating potential of optimal fertilisation in boreal forests, uncertainty remains about the variation in effect size under different environmental conditions, particularly with respect to site productivity. Also, it is still unclear to what extent experimental findings can be translated into practice, especially regarding fertilisation frequency and the question whether plot-level results remain valid at the stand scale.

A major step towards implementation in operational forestry in Sweden occurred in the early 2000s with the establishment of two new nutrient optimisation experiments in young Norway spruce forests (Bergh et al., 2008), whose long-term results are presented here. The first study aimed at testing the effects of fertilising 0.1 ha plots at one-, two-, and three-year intervals, and was replicated at five sites in southern and central Sweden (hereafter referred to as *interval trial*). The second study investigated whole-stand fertilisation using a two-year interval, a frequency that is deemed feasible in operational forestry (Nilsson and Fahlvik, 2006). This experimental approach was replicated at four sites in southern and central Sweden (hereafter referred to as *practice-oriented trial*). An early assessment (first five years) of the interval trial revealed that yearly and two-yearly fertilisation greatly stimulated stem growth to a similar degree, with slightly lower yields in the three-yearly schedule (Bergh et al., 2008). In this study, we extend the early time series of both the interval and practice-oriented trial and present novel, previously unpublished data on growth and yield following a >10-year fertilisation period when the stands had reached canopy closure at an age of 23–33 years. The practice-oriented trial was designed as a complementary study on a larger spatial scale in close alignment with forest management practices to test the operational feasibility. We hypothesised i) that based on our preliminary findings, a two-year fertilisation interval is sufficient for maximising growth and yield gains in young Norway spruce stands, ii) two-yearly fertilisation will result in similar wood yields at the plot level (interval trial) and the stand level (practice-oriented trial), and iii) that trees at less productive sites will be more efficient at converting N to biomass than those at more productive sites, *i.e.* a negative correlation between N use efficiency and site productivity (using site index H100 as a proxy).

2. Material and methods

2.1. Site and stand characteristics

The study sites are located in southern (Ebbegärde, Toftaholm, Tranemo) and central Sweden (Mölnbacka, Gullspång, Hällefors, Grängshammar, Valbo, Bräcke; Fig. 1). All stands grow on upland soils with forest continuity, which have developed into various forms of podzols (IUSS Working Group WRB, 2015). The Bräcke site is dominated by a shallow, cobble-rich, glacial till with silty soil texture. The soils at Valbo, Grängshammar, Toftaholm, Gullspång, Hällefors and Tranemo have developed from glacial sandy till, while the soil at Mölnbacka formed from clayey glacial till. The soil at Ebbegärde is a sandy glacial till with elements of ice river gravel sediment. Mor humus prevails at most study sites but Grängshammar, Valbo and Mölnbacka feature a mosaic of mor and moder. The length of the growing season ranges from ca. 155 days at Bräcke to 200 days at Ebbegärde, while precipitation ranges from 500 mm at Ebbegärde to ca. 900 mm for Tranemo (see Table 1). The site fertility index varied from G22 at Bräcke to G33 at Toftaholm (Table 1, Hägglund and Lundmark, 1977). All sites were planted with Norway spruce (*Picea abies* (L.) Karst.) of appropriate provenances. Bräcke was established in 1983 and Toftaholm in 1993, while the other sites were planted between 1987 and 1992.

2.2. Experimental design

The overarching study consisted of two experimental setups, the interval trial and practice-oriented trial (Fig. 1). The experimental design of the interval trial is described in detail in Bergh et al. (2008). Briefly, each fertilisation treatment (described below) was replicated in

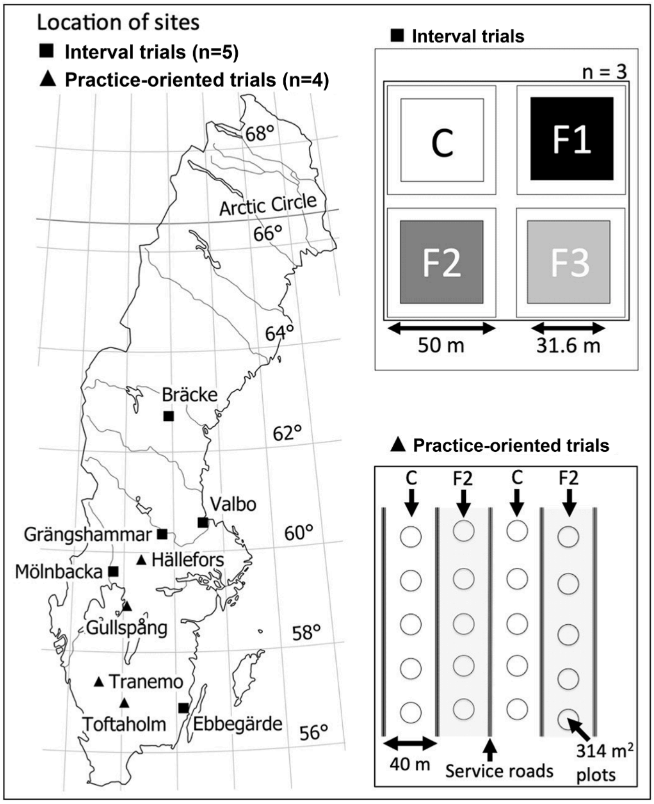

Fig. 1. Map of Sweden (GSD-Maps of Sweden © Lantmäteriet) with the locations of the 9 young Norway spruce forests (left) and the experimental design for the two fertilisation trials in this study (right). Each of the sites in the interval trials (squares) consist of three blocks with control plots and fertilisation with one-, two-, or three-year intervals (C, F1, F2, F3) replicated at five sites. The practice-oriented trials (triangles) consist of large areas fertilised with two-year intervals along service roads, and control areas without fertilisation, replicated at four sites.

three blocks at each of the five sites with a plot size of 50×50 m, except for Ebbegärde and Bräcke, where the plot size was 40×40 m and each plot contained an inner plot (1000 m^2) surrounded by a buffer zone. The total area of each site was ca. 4.5 ha at Mölnbacka, Grängshammar and Valbo, and ca. 3 ha for Ebbegärde and Bräcke. Fertiliser was applied by hand.

In the practice-oriented trial, the fertilisation treatment was equivalent to the F2 treatment in the interval trial, but the first three applications were done with a fan spreader mounted on a tractor along a GIS-planned service road system with 40 m between the roads (Fig. 1). The last three applications were carried out by helicopter. Both methods are known to provide precise and even fertiliser distribution. Fertilisation was conducted six times between 2003 and 2013 and the total fertilised area was around five hectares at each site, which corresponds to typical stand areas in Swedish plantation forestry. Circular measurement plots (314 m^2, $n = 20$) were randomly distributed in the fertilised and unfertilised areas, centrally between the service roads (Fig. 1).

2.3. *Fertilisation treatments*

The fertilisation treatments build on the concept of optimal fertilisation, based on foundational work in the laboratory (Ericsson and Kähr, 1993) and field experiments (Linder, 1990; Stockfors et al., 1997). In these prior studies, threshold leaf concentrations and proportions of the essential nutrients were established to eliminate nutrient limitations to growth, while minimizing nutrient leaching. Based on nutrient analyses of previous-year needles, the fertiliser composition was adjusted each year to meet the targeted needle N concentrations and N-related nutrient ratios (Bergh et al., 2008, 1999; Linder, 1995).

Besides the unfertilised control (C), fertilisation treatments were applied every year (F1), every second year (F2), or every third year (F3), prior to budbreak in May each year. We used commercial solid fertilisers (Yara AB, Malmö, Sweden) containing ammonium nitrate (NH_4NO_3) as N source, monocalcium phosphate ($Ca(H_2PO_4)_2$) as P source and K supply in the form of potassium nitrate (KNO_3) (supplementary Tables 1 and 2). The fertilisation of the interval trials started in 2002 (Fig. 1, Table 2, see supplementary Table 1 for complete nutrient composition) and ended in 2014. At the four northernmost interval fertilisation sites (Bräcke, Grängshammar, Valbo, and Mölnbacka), the initial amounts of N were 100, 150 and 180 kg N ha^{-1} for the F1, F2 and F3 treatments respectively, while the southernmost site Ebbegärde received 75, 125 and 150 kg N ha^{-1}. Following the start of fertilisation in 2002, needle N-concentration increased drastically at all four sites (Bergh and Linder, 2006), whereas P declined below target values in relation to N. A high P product was therefore used in subsequent fertilisations, which also contained higher concentrations of K. Since then, all N-based nutrient ratios remained at or above target values. Informed by foliar nutrient status and lysimeter monitoring data to minimise N-leaching, from 2005 onwards the amount of fertiliser was reduced to 75, 125, and 150 kg N ha^{-1} in the F1, F2 and F3 treatments, respectively (matching the amounts applied at the southernmost site Ebbegärde from the start).

Fertilisation in the practice-oriented trial started in 2003 with a total of 150 kg of N ha^{-1} supplied every second year until 2013. The applied amount of N remained the same at all four sites, but P and K were adjusted occasionally to maintain target values of the associated foliar N-based nutrient ratios (Table 2, see supplementary Table 2 for

Table 1
Location, climate, and site index (dominant height at 100 years) for the 9 sites.

Experimental site		Latitude	Longitude	Elevation (m.a.s.l.)	Precipitation (mm a^{-1})	Humidity* (mm a^{-1})	Vegetation period (days)	Mean annual temperature (°C)	Site index (H100)	Initial standing volume (m^3 ha^{-1})
Interval trial										
	Bräcke	62°43′N	15°51′E	390	650	50–100	155	2	G22	8.8±1.5
	Grängshammar	60°21′N	15°31′E	200	700	100–150	170	4	G24	9.1±1.0
	Valbo	60°34′N	17°11′E	40	700	50–100	175	5	G24	2.4±0.3
	Mölnbacka	59°36′N	13°34′E	90	800	100–150	180	5	G26	3.6±0.3
	Ebbegärde	56°53′N	16°15′E	35	500	<50	200	6.5	G29	2.9±0.5
Practice-oriented trial										
	Hällefors	59°86′N	14°68′E	290	750	100–150	175	5	G26	2.2±0.2
	Gullspång	58°93′N	14°16′E	110	600	50–100	180	6	G28	2.5±0.2
	Tranemo	57°44′N	13°12′E	150	900	150–200	190	6.5	G32	3.6±0.3
	Toftaholm	57°00′N	14°08′E	160	800	100–150	180	5.5	G33	3.4±0.2

* Humidity during the growing season according to the Swedish Institute for Meteorology and Hydrology (SMHI).

Table 2

Number of fertilisation events and cumulative addition of nitrogen (N), phosphorus (P), and potassium (K) per hectare for each of the treatments (F1, F2 and F3) at the five sites of the interval fertilisation trial (2002–2014) and the four sites of the practice-oriented trial (2003–2013).

Experimental site	Treatment	Fertilisations n	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})	N:P	N:K	K:P
Interval trial								
Bräcke	F1	13	1075	246	568	4.4	1.9	2.3
	F2	7	925	198	458	4.7	2.0	2.3
	F3	5	780	164	261	4.8	3.0	1.6
Valbo, Grängshammar, Mölnbacka	F1	12	1050	239	561	4.4	1.9	2.3
	F2	6	925	198	458	4.7	2.0	2.3
	F3	4	780	164	261	4.8	3.0	1.6
Ebbegärde	F1	12	975	347	1107	2.8	0.9	3.2
	F2	6	850	291	931	2.9	0.9	3.2
	F3	4	725	169	328	4.3	2.2	1.9
Practice-oriented trial								
Hällefors	F2	6	850	163	154	5.2	5.5	0.9
Gullspång	F2	6	850	151	120	5.6	7.1	0.8
Tranemo	F2	6	850	187	308	4.5	2.8	1.6
Toftaholm	F2	6	850	187	308	4.5	2.8	1.6

complete nutrient composition). At Toftaholm and Tranemo, 187 kg ha^{-1} of P and 308 kg ha^{-1} of K were added, at Gullspång 151 kg ha^{-1} of P and 120 kg ha^{-1}of K were supplied, while Hällefors received 163 kg ha^{-1} of P and 154 kg ha^{-1} of K.

2.4. *Measurements and growth estimates*

Standing volume and periodic annual increment were determined according to the methodology of the Swedish National Forest Inventory, based on repeated measurements of tree height and diameter at breast height (DBH) (Brandel, 1990). Tree height recordings also form the basis for the site index calculations following Hägglund and Lundmark (1977). In the interval fertilisation trials, measurements were made after the 2001 or 2002, 2005 or 2006, 2011, and 2016 growing seasons. DBH was measured for all trees in the inner plots, and height was measured for a sample of trees (ca. 13% of the total) representatively selected from the diameter distribution in the stands. Volumes of the remaining trees were estimated by linear regression based on the treatment and site-specific relationships between volume and DBH ($r^2 \sim 0.99$ for diameter classes > 5 cm).

Stem volume in the practice-oriented trials was derived from DBH and height for all trees in the sample plots. Stem volume was measured after the 2002 or 2003, 2007 or 2008, 2013 or 2014, and 2017 growing seasons, and volume growth was calculated as the difference in volume between measurements.

2.5. *Nitrogen use efficiency*

We calculated the amount of stemwood volume produced per mass unit of N added, hereafter referred to as N use efficiency (NUE), to account for differences in total N addition rates between fertilisation intervals and the two different experimental setups (interval fertilisation trial vs. practice-oriented trial). NUE was calculated as the difference in stem volume between the control and each of the fertilisation treatments divided by the total amount of N added.

2.6. *Statistical analysis*

All statistical modelling was performed using the R software environment (R Core Team, 2022).

Periodic annual increment in the interval and practice-oriented trials was analysed using generalised additive mixed models (GAMM) with a Tweedie error distribution (R package *mgcv*, Wood, 2011). The GAMMs contained ‘fertilisation treatment’ (F1, F2, F3) as parametric term and a smoothing term (thin plate regression splines) for ‘time’ including ‘fertilisation treatment’ as a by-variable to allow for factor-smooth interactions, *i.e.* separate smoothers for each fertilisation treatment. The random component consisted of ‘block’ nested within ‘site’. An autocorrelation function highlighted serial correlation in the residuals of the GAMM related to the interval fertilisation trials, which we modelled by incorporating an autocorrelation structure of order 1 (AR1). We detected no serial correlation in the GAMM for the practice-oriented trials.

Stem volume yield and NUE determined at the end of the trials were analysed using linear mixed effects (LME) models (R package *nlme*, Pinheiro et al., 2022). These LME models contained ‘fertilisation treatment’ as predictor and a nested random term consisting of ‘block’ within ‘site’. We used graphical model validation tools to check the underlying assumptions of homoscedasticity and normality of the model errors (plots of the normalised residuals vs. fitted values and quantile-quantile plots). The residual plots did not indicate any gross violations of the model assumptions. A backwards selection procedure based on likelihood ratio tests was used to assess the overall significance of the ‘fertilisation treatment’ effect. A *post hoc* analysis using Tukey contrasts (all possible pairwise comparisons) was performed to determine significant differences at $\alpha = 0.05$ between the levels of the ‘fertilisation treatment’ (fertilisation frequencies) in the interval fertilisation trial (R package *emmeans*, Lenth, 2022).

3. Results

3.1. *Effects of different fertilisation intervals on periodic annual increment (PAI), stem volume yield and nitrogen use efficiency (NUE)*

In the interval fertilisation trial, all nutrient optimisation treatments significantly increased PAI relative to the control ($F_{3,285} = 39.11$, $P < 0.001$, Fig. 2a, Table 3). At the end of the study period, the F1 and F2 treatments caused similarly large stimulations of PAI between 105 % and 93 %, respectively (C: 11.0 m^3 ha^{-1} yr^{-1}, F1: 22.7 m^3 ha^{-1} yr^{-1}, F2: 21.4 m^3 ha^{-1} yr^{-1}, F3: 19.8 m^3 ha^{-1} yr^{-1}). The effect size in the F3 treatment (+79 %) was significantly lower compared to the F1 and F2 treatments (Table 3). The random variation introduced by the site effect varied with treatment from −4.0 to +2.5 m^3 ha^{-1} yr^{-1} and was consistently above the mean at two central Swedish sites (Mölnbacka, Grängshammar), close to the mean at the northernmost and southernmost sites (Bräcke, Ebbegärde) and always well below average at the remaining central Swedish site (Valbo) (Fig. 2a). The nutrient-driven increases in PAI translated into significantly larger stem volume yields relative to the control ($L = 65.14$, $df = 3$, $P < 0.001$). Two years after the

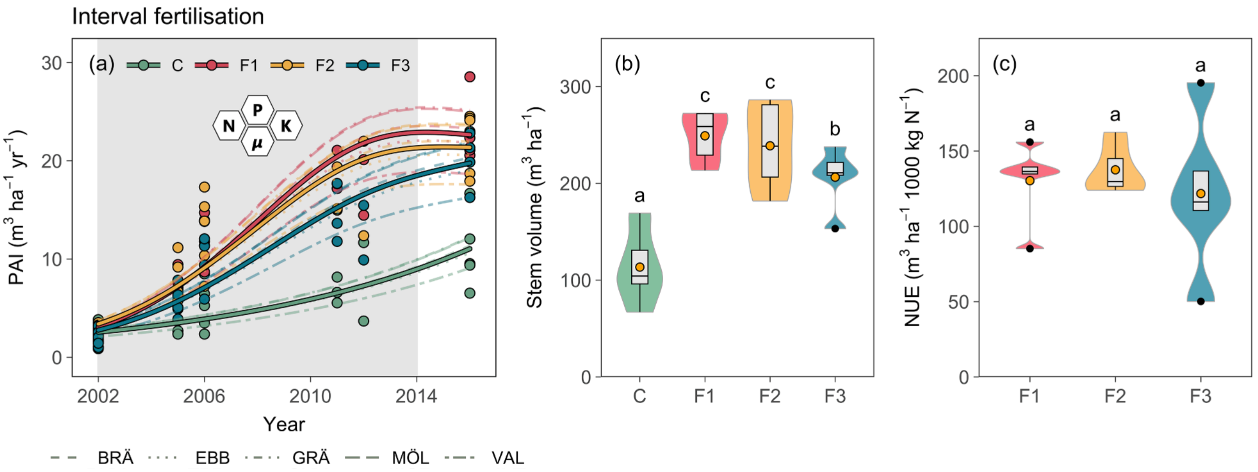

Fig. 2. Results of an interval fertilisation trial comprising five young Norway spruce stands along a 700 km north-south gradient in Sweden. At each stand, unfertilised control plots (C) were contrasted with plots receiving NPK fertiliser containing additional macro- and micronutrients every year (F1), every two years (F2) or every three years (F3) between 2002 and 2014, followed by volumetric yield measurements in 2016. **(a)** Periodic annual increment (PAI); filled symbols indicate stand means per treatment, the curves represent generalised additive mixed model (GAMM) fits. The solid lines indicate the mean fit (main effect) for each treatment level, while the broken lines indicate the fits of the individual sites, *i.e.* the random variation around the mean model fit (BRÄ = Bräcke, EBB = Ebbegärde, GRÄ = Grängshammar, MÖL = Mölnbacka, VAL = Valbo). The grey-shaded area indicates the fertilisation period. **(b)** Stem volume yield of standing trees at the final assessment after the 2016 growing season, **(c)** nitrogen use-efficiency (NUE) across the fertilisation treatments defined as the difference in stem volume yield between each fertilisation treatment and the control divided by the total N addition × 1000 kg N. Filled orange circles within boxplots denote the mean. The violin plots surrounding the boxplots visualise the distribution of the data. Different lower-case letters in (b) and (c) indicate statistically significant differences at α = 0.05 (*post hoc* comparison using Tukey contrasts).

Table 3
Results from a *post hoc* analysis applied to the GAMM of the PAI (m^3 ha^{-1} yr^{-1}) related to the interval trial. Estimated differences in PAI between treatments and their standard errors (SE) are given on the log scale. *P*-values were adjusted for multiple testing using the false discovery rate method (Benjamini and Hochberg, 1995). SE = standard error, *t* = *t*-value, *P* = *P*-value.

Contrast	Estimate	SE	*t*	*P*
C – F1	−1.072	0.088	−12.13	**<0.001**
C – F2	−1.023	0.089	−11.49	**<0.001**
C – F3	−0.772	0.092	−8.39	**<0.001**
F1 – F2	0.049	0.095	0.51	0.6088
F1 – F3	0.300	0.098	3.07	**0.0036**
F2 – F3	0.251	0.098	2.56	**0.0133**

final fertiliser application, we observed 120 % and 110 % greater stem volume yields in the F1 and F2 treatments compared to the unfertilised control (Fig. 2b, see supplementary Table 3 for site-level results). In comparison, the effect of the F3 treatment was significantly smaller, but still represented an 82 % increase in stem volume yield over the control (Fig. 2b). We accounted for the different amounts of total N, that inevitably result from the various fertilisation intervals, by calculating the nitrogen use efficiency (NUE; increase in stem volume yield over the control per unit of N applied). Average NUE values did not differ significantly across fertilisation intervals ranging from 121 to 138 m^3 ha^{-1} 1000 kg N^{-1} with a mean across fertilisation treatments of 130 m^3 ha^{-1} 1000 kg N^{-1} (Fig. 2c).

In the practice-oriented trial, with only a two-year fertilisation regime (F2 treatment), nutrient addition significantly increased PAI by 95 % from 12.6 m^3 ha^{-1} yr^{-1} in the control to 24.6 m^3 ha^{-1} yr^{-1} in the treated plots ($F_{1,58} = 20.4$, $P < 0.001$; Fig. 3a). This increase was similar in magnitude to the effect of the F2 treatment in the interval trial. The site-related random variation in PAI was rather small fluctuating only *ca.* 1.2 m^3 ha^{-1} yr^{-1} around the control mean and *ca.* 2.3 m^3 ha^{-1} yr^{-1} around the F2 mean (with Gullspång and Hällefors consistently slightly above the mean response, and Tranemo and Toftaholm somewhat below, Fig. 3 a). The fertiliser-induced stimulation of PAI translated into a significant increase in stem volume yield by 114 % ($L = 84.7$, $df = 1$, $P < 0.001$), which agrees well with the gain seen in the F2 treatment in the interval trial (Fig. 3b, see supplementary Table 3 for site-level information). The mean NUE was 132 m^3 ha^{-1} 1000 kg N^{-1} (Fig. 3c).

3.2. Relationship between nitrogen use efficiency and site index H100

In the F1 treatment, NUE declined with an average slope of 9.8 m^3 ha^{-1} 1000 kg N^{-1} with increasing sited index H100 (Fig. 4). However, this relationship was only marginally significant (t = -2.85, $df = 3$, P = 0.065) and explained little of the variation ($r^2 = 0.13$). The pooled F2 observations from the interval trial and the practice-oriented trial showed a statistically significant decrease in NUE of 6.46 m^3 ha^{-1} 1000 kg N^{-1} per unit increase in site index (Fig. 4). This statistically significant relationship (t = -4.92, $df = 7$, $P = 0.002$) explained 39 % of the variation (Fig. 4). NUE also showed a strong decline in the F3 treatment up to a site index of 26, but a fairly large NUE value of around 180 m^3 ha^{-1} 1000 kg N^{-1} coinciding with the highest site index in this treatment (H100 of 29) disrupted the downward trend, so that no statistically significant relationship emerged (Fig. 4).

4. Discussion

Late-rotation fertilisation, often a single application of 150 kg N ha^{-1}, is a common forest management practice in Nordic countries that boosts stemwood growth in Norway spruce by roughly 30 % (Hedwall et al., 2014b; Ingerslev et al., 2001). However, fertilisation efficiency is closely linked to nutrient demand and growth potential, and thus stand developmental stage, as evidenced by higher NUE in younger stands compared to older ones under otherwise similar site conditions (Hyvönen et al., 2008). In the present study, we therefore evaluated the potential growth gains from early and repeated fertilisation of young Norway spruce stands across Sweden. Since the forest soils in this region are commonly nutrient-deficient (Tamm, 1991), we contrasted one-, two- and three-year fertilisation intervals (F1, F2, F3) to determine the treatment frequency that maximises growth and thus provide decision-making support for forest managers.

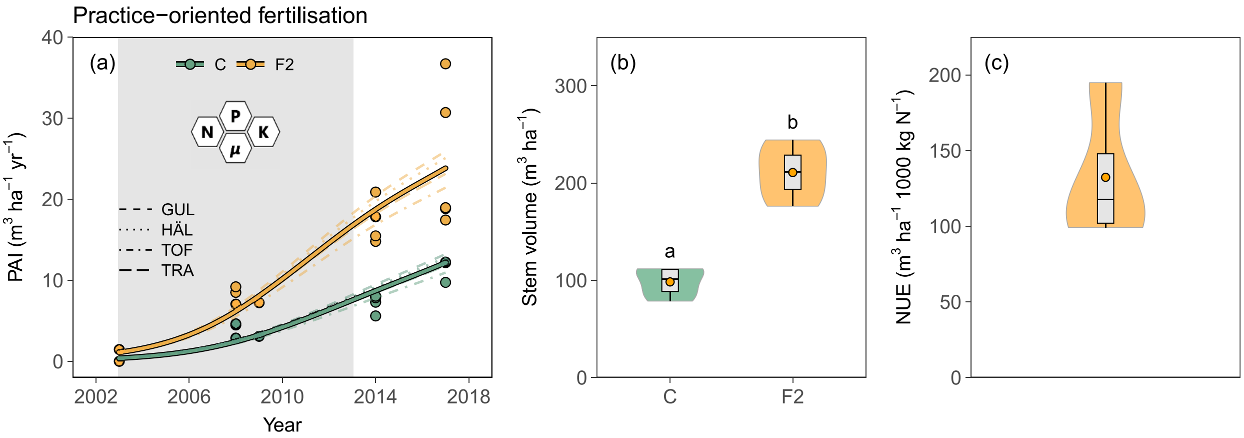

Fig. 3. Results of a practice-oriented fertilisation trial comprising four young Norway spruce stands in mid and southern Sweden. At each stand, unfertilised control plots (C) were contrasted with plots receiving NPK fertiliser containing additional macro- and micronutrients every two years (F2) between 2003 and 2013, followed by volumetric yield measurements after the 2017 growing season. **(a)** Periodic annual increment (PAI); filled symbols indicate stand means per treatment, the curves represent generalised additive mixed model (GAMM) fits. Solid lines indicate the mean fit and the broken lines show the site-level random variation (GUL = Gullspång, HÄL = Hällefors, TOF = Toftaholm, TRA = Tranemo). The grey-shaded area indicates the fertilisation period. **(b)** Box-and-violin plots of stem volume yield of standing trees at the final assessment after the 2017 growing season, **(c)** box-and-violin plot of the nitrogen use-efficiency (NUE) in the F2 treatment defined as the difference in stem volume yield between the fertilisation treatment and the control divided by the total N addition × 1000 kg N. Filled orange circles within boxplots denote the mean. The violin plots surrounding the boxplots visualise the distribution of the data. Different lower-case letters in (b) indicate statistically significant differences at $\alpha = 0.05$ (*post hoc* comparison using Tukey contrasts).

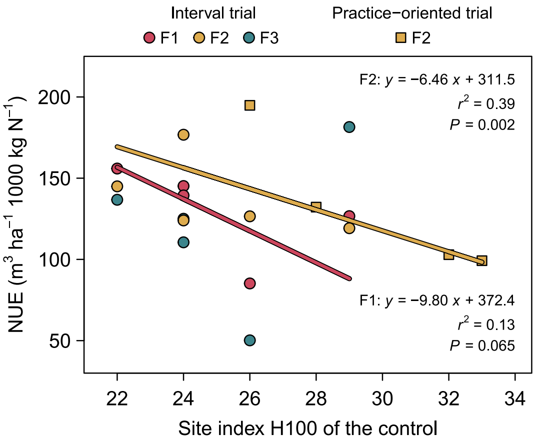

Fig. 4. Nitrogen use efficiency (NUE) as a function of the site index (H100) of the control (see Table 1). Filled circles indicate NUE data related to the five interval trial sites. Filled yellow rectangles depict the NUE observations in the practice-oriented trial (consisting of the F2 treatment only). The red regression line displays the marginally significant NUE-site index relationship in the F1 treatment. The yellow regression line indicates the statistically significant NUE-site index relationship in the F2 treatment, pooled across the two trials (interval trial, practice-oriented trial). There was no significant relationship in the F3 treatment.

4.1. *Fertilisation effects on PAI, stem volume yield and NUE*

Our results show that repeated fertilisation of young Norway spruce stands at yearly or two-yearly intervals (F1 and F2 treatments) can double stemwood production within ca. 15 years across a wide range of site and climate conditions in northern Europe (Figs. 2 and 3). Noticeable fertilisation effects on growth can be expected to emerge within 3–4 years after the first application as was shown in an early-phase assessment of our experiments (Bergh et al., 2008). Five years after the start of the interval trial, Bergh et al. (2008) reported similar fertiliser-driven stimulation in current annual increment (F1: 123 %, F2: 132 %, F3: 77 %) but somewhat lower increases in stemwood yield over the control (F1: 79 %, F2: 89 %, F3: 42 %) compared to our final assessment 14 years after the start of the study. The same early evaluation by Bergh et al. (2008) showed a 134 % increase in current annual increment after three growing seasons in the practice-oriented trial compared to a 95 % stimulation of PAI seen in our study while the fertiliser-related increase in stemwood volume of 108 % seen in the early phase was close to the 114 % stimulation recorded in our final 2017 assessment. Stand fertilisation at two-yearly intervals is a viable option both operationally and economically (Nilsson and Fahlvik, 2006), and our multi-site findings of similar effect sizes across the F1 and F2 treatments confirm our first hypothesis that a two-yearly interval is sufficient to achieve maximal growth stimulation and thus lend strong support to the implementation of such a fertilisation schedule where appropriate. However, since the three-yearly fertilisation frequency tested with the F3 treatment still resulted in about 80 % stimulation of PAI and volume yield relative to the unfertilised control, it also provides a viable management option, especially where economic or logistic constraints prohibit more frequent applications. In support of our second hypothesis, the similar fertiliser effect sizes of the F2 treatment across the interval and practice-oriented trials indicate that plot-level findings hold at the stand-level, providing good prospects for adoption in forestry practice.

The extent of the site-related random variation in PAI was largely driven by the consistently lower values at the Valbo site (close to the eastern coastline in mid-Sweden), which are probably linked to the edaphic conditions. The stand grows on a histosol, characterised by periods of stagnant water with little solute movement and anaerobic conditions when rainfall is abundant, but during dry periods the peaty topsoil quickly becomes hydrophobic hindering infiltration and thus soil water replenishment (Orfánus et al., 2021). Such a combination of soil factors is likely to hamper tree growth. The remaining site-related random variation was rather small and showed no clear latitudinal pattern as one might have expected due to the stronger N-limitation in northern vs. southern regions (Högberg et al., 2021), mainly driven by cooler temperatures and lower anthropogenic N deposition up North (de Vries et al., 2014; Solberg et al., 2009). Large differences in growth responses to fertilisation related to this N-limitation gradient have already been observed in pioneering studies where yearly nutrient optimisation increased stem volume production 4.7-fold at a site in northern Sweden vs. 2.4-fold at a southern site (Bergh et al., 1999). We therefore suspect that in our study local variations in site conditions have overshadowed the latitudinal N-limitation gradient. The interplay between temperature, evaporative demand, precipitation, and edaphic conditions can strongly influence the fertiliser-growth response directly or indirectly through changes in soil water availability (Bergh et al., 1999). Previous experiments including combined fertilisation and irrigation treatments showed that water availability limited the growth response to fertilisation at a site in southern but not in northern Sweden (Bergh et al., 2005, 1999; Lim et al., 2015). Climate change-induced water shortages will probably become more frequent in southern Sweden in the future (Teutschbein et al., 2023), which needs to be factored into forest planning and decision-making. In areas already prone to water deficit today, such as the region around our southernmost site at Ebbegärde (Table 1), where water deficits occur on a regular basis during the dry summer period, water availability will increasingly control the magnitude of the fertiliser effect in the future. Although the fertiliser-growth response at this driest site of ours was not far below the overall mean (Fig. 2a), it is reasonable to assume greater stimulation under more favourable water availability.

Fertilisation frequency certainly matters and our findings and those of others indicate that the highest stemwood yields on nutrient-poor boreal soils can be achieved with frequent nutrient additions. Similar production increases in earlier experiments with comparable fertilisation regimen have been reported for common conifers in Canada (Western red cedar, Western hemlock, Bennett et al., 2003; white spruce, Brockley, 2010, Lodgepole pine, Brockley, 2003, Engelmann spruce, Brockley, 1992). However, even one-off nutrient additions can have long-lasting effects as has been shown for western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), whose growth was still stimulated by 62 % and 50 %, respectively, 10 years after fertilisation (Bennett et al., 2003). Similar carry-over effects were reported for young Scots pine and Norway spruce stands in central Sweden still benefiting from fertiliser applications in the previous rotation (From et al., 2015). Therefore, it is not surprising that chronic nutrient enrichment through agricultural land use can create soil nutrient legacies that might persist over decades up to centuries after reforestation and may make fertiliser application entirely redundant (Falkengren-Grerup et al., 2006; Svensson et al., 2023), emphasising the need to take land use history into account in forest management and planning. Our interval trial resulted in vastly differing N loadings. To evaluate the effect of varying fertilisation intervals, we accounted for differences in total N addition by calculating NUE (expressed as stemwood yield per unit mass of added N) and found no statistically significant differences across fertilisation schedules (Fig. 2c), indicating that the yield differences between fertilisation intervals were only due to differences in the total amount of N added. Our relatively high NUE values imply that just about 7–8 kg N ha^{-1} are needed to produce one extra m^3 of stemwood per hectare (Figs. 2 and 3). The traditional late-rotation fertilisation (during the last decade of the rotation) has been reported to increase stemwood yield of Norway spruce by 8 to 15 m^3 ha^{-1} (Hedwall et al., 2014a; Nohrstedt, 2001), which translates into 10–19 kg N ha^{-1} to produce one extra m^3 of wood per hectare. These figures indicate that a much larger proportion of fertiliser-N is converted to biomass when added early in the rotation compared to late applications and hence provides a strong argument for starting forest fertilisation already in juvenile stands. The fairly high NUE in our study may also be partly due to the release from co-limitations by P and K or micronutrients included in the fertiliser (Hyvönen et al., 2008; Nohrstedt, 2001). The similarity of NUE values observed across fertilisation schedules indicates that not even the greatest fertiliser inputs associated with annual application led to N saturation in these forest soils, implying that soil N losses through leaching or nitrous gas emissions are unlikely to increase drastically as a result of intensive fertilisation. This conjecture is corroborated by low N-leaching five years after the start of our trials (Bergh et al., 2008) and supported by recent findings from a young Norway spruce stand where fertilisation equivalent to our F2 treatment only caused a short-lived increase in N_2O emissions (Håkansson et al., 2021). The clear indications of tight N-cycling at our sites together with the strong fertiliser growth response suggest great C mitigation potential of repeated forest fertilisation in aggrading Norway spruce stands. This is in line with previous studies showing that fertilisation can enhance ecosystem C sequestration above- and belowground and therefore help mitigate climate change (Blaško et al., 2022; Hyvönen et al., 2008; Maaroufi et al., 2015). The probable synergy between nutrient addition and rising atmospheric CO_2 may further amplify forest C mitigation given the strong stimulation of Norway spruce photosynthesis under experimentally elevated CO_2 (Bader et al., 2016). A recent study on long-term nutrient enrichment in young Norway spruce stands including some of our sites, demonstrated a 47 % increase in ecosystem C stocks after 13 years of annual fertiliser applications, dominated by increases in above- and belowground tree biomass (Blaško et al., 2022). The same study also found a fertiliser-related 28 % rise in ecosystem N stocks largely driven by aboveground N accumulation in stem wood and bark suggesting that logging residue from typical stem-only harvests (without debarking) is unlikely to cause high N leaching (Blaško et al., 2022). The positive effects of early and repeated fertilisation must be weighed against i) greater economic risks associated with the relatively long investment times when fertilising young forests compared to late-rotation fertilisation (Andrew Stainback and Alavalapati, 2002), ii) environmental risks such as lower biodiversity (Hedwall et al., 2014a; Hedwall et al., 2014b), shifts in soil microbial community composition and related changes in soil N dynamics (Blaško et al., 2013), and iii) increased leaching at the land-scape level if fertilisation becomes more widespread and shortens rotation times in the future (Futter et al., 2010; Gundersen et al., 2006).

4.2. Relationship between nitrogen use efficiency and site index H100

Initial site productivity strongly affects the magnitude of the fertiliser-driven growth stimulation with less productive sites responding more vigorously to nutrient enrichment than those with higher baseline productivity (Blaško et al., 2022; Saarsalmi and Mälkönen, 2001). This is consistent with the observed decline in NUE with increasing site index (proxy for site productivity) in the F1 and F2 treatments of our study (Fig. 4). Productive sites with higher site index tend to have more favorable soil N availability, resulting in less pronounced responses to N-fertilisation alone, *i.e.* relatively lower NUE (Hyvönen et al., 2008; Saarsalmi and Mälkönen, 2001). However, NPK-fertilisation has been reported to result in high NUE also in N-rich soils due to the removal of P and K limitation and NUE even showed a slightly decreasing trend with increasing C/N ratio across Norway spruce and Scots pine stands of varying age (Hyvönen et al., 2008). Yet, for young Norway spruce stands, our findings and those of Blaško et al. (2022) indicate that the negative correlation between NUE and baseline site productivity persists even when a comprehensive nutrient mix is added (NPK plus other macro- and micronutrients), which may be attributable either to a generally more favourable baseline nutrient availability at the more productive sites or to the deficiency of a certain nutrient not contained in the fertiliser mix.

5. Conclusions

By providing novel, much-needed knowledge on the large-scale and long-term effects of repeated fertilisation of young Norway spruce, we show that much higher yields can be attained through early and repeated fertilisation compared to traditional fertilisation regimes in use today. The large proportion of added N that was converted to stem biomass in our study indicates greater N-retention in the system compared to traditional late-rotation fertilisation implying small N leaching and gaseous losses despite higher total N addition rates. The combination of high NUE with the possibility to add more N without heightened risk of leaching clearly points towards the large swaths of low-productive Norway spruce forest in northern Fennoscandia as promising areas for increased biomass production and CO_2 mitigation through repeated fertilisation. However, forest policy-makers and managers should carefully consider prior land use history and site characteristics (e.g. soil type, water availability, baseline productivity) when planning forest fertilisation activities because additional management interventions, such as supplementary irrigation in drought-prone areas, may be required to fully exploit the growth promoting fertiliser potential. With dry spells becoming more frequent in many places, such long-term forest fertilisation trials offer a unique opportunity to shed light on the poorly understood interaction between soil nutrient supply and drought and its effect on the growth resilience of forests.

CRediT authorship contribution statement

Carl Svensson: Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **Martin Karl-Friedrich Bader:** Formal analysis, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Benjamin Forsmark:** Formal analysis, Data curation, Writing – review & editing. **Urban Nilsson:** Data curation, Writing – review & editing. **Tomas Lundmark:** Writing – review & editing, Funding acquisition. **Annika Nordin:** Writing – review & editing, Funding acquisition. **Johan Bergh:** Methodology, Conceptualization, Data curation, Funding acquisition, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Annika Nordin reports a relationship with Stora Enso AB that includes: employment.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121425.

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